

**LIFE HISTORY OF *DOHRNIPHORA CORNUTA* (BIGOT)  
(DIPTERA: PHORIDAE), A FILTH-INHABITING  
HUMPBACKED FLY**

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*Abstract.*—The literature on the life history and immature stages of *Dohrniphora cornuta*, a synanthropic, filth-inhabiting, humpbacked fly, is reviewed and summarized, and observations on laboratory rearings are presented. Adult females and larvae consume many kinds of dead and decaying animal and plant tissues, but apparently both are facultative predators of insects when other foods are not available. Adult males are apparently nectar feeders, and they are much shorter lived than females. Pest status, reproductive behavior, and life history parameters are compared with other phorid species, and the evolution of non-genitalic sexual structures is discussed.

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*Dohrniphora cornuta* (Bigot) is one of the more conspicuous and widespread species of Phoridae, although Schmitz (1951) stated that in Europe adults are found only during warm periods, and the species seems to prefer warmer regions. According to Borgmeier's (1968) world catalog, its distribution is cosmopolitan, and it has masqueraded under at least 13 species names and 4 generic names. Many anecdotal reports of food sources and breeding sites have appeared in the literature, and they leave little doubt that Schmitz (1951) was correct in referring to the larvae as indiscriminate saprophages, although they sometimes exhibit facultative predatory behavior. Medical, veterinary, and economic aspects of the species' life history are evident from its generally synanthropic tendencies (Bohart and Gressitt, 1951; Schmitz, 1951; Weiss, 1911) and from reports of adult females biting man (Schmitz, 1938, 1951) and of larvae causing myiasis in cattle (Patton, 1922), living in human excrement (Skidmore, 1978) and other types of filth (Bohart and Gressitt, 1951), and helping to stabilize psychodid populations through predation and competition in a trickling filter sewage bed (Kloter et al., 1977). Recently, specialists at a United States Food and Drug Administration laboratory in Los Angeles, California, performed a filth extraction procedure on hermetically sealed barbecue sauce imported from the Republic of China that yielded an adult phorid, which was identified as a male *D. cornuta* by B. V. Brown (University of Alberta) (J. Madenjian, pers. comm.).

Larvae of *Dohrniphora cornuta* have been found in many kinds of decaying plant and animal tissues. Disney (1983) reported the species breeding in compost, and Kloter et al. (1977) reported larvae feeding on fresh cow manure and the film that develops in sewage beds. Reports have been published of larvae found in decaying onions (Johannsen, 1935), of specimens reared from cow peas (Malloch, 1912), and of the species breeding in rotting rice bran (Disney, 1983). Schmitz (1951) made mention of larvae found in melons and wasp nests. Jones (1918) reported the species breeding in insect remains in pitcher plants (*Sarracenia flava* L.), and he reared the species on dead grasshoppers (Bohart and Gressitt [1951] reported that *D. cornuta*

has been reared from living grasshoppers, but they did not cite a reference). Brues (1924) reported on a large series of specimens collected from a box of termite-eaten papers that also contained a rat's nest and concluded that larvae develop in decaying animal matter, but Borgmeier (1925) collected an adult specimen from a *Eutermes* nest and surmised that the species is termitophilic. Bigot (1890) reported on specimens bred from a tachinid parasite of the silkworm, but Townsend (1893) doubted the veracity of this claim. Specimens have been bred from dead snails (Schmitz, 1915; Brues, 1925), soured milk (Schmitz, 1917), a rotting egg of the great tit (*Parus major cinereus* Viellot) (de Meijere, 1938), and tainted flesh of dead rodents (Weiss, 1911).

In their report on the filth-inhabiting flies of Guam, Bohart and Gressitt (1951) mentioned that *D. cornuta* is especially attracted to decaying molluscs, and like its associate, *Megaselia scalaris* (Loew), its omnivorous tastes and domestic habits make it a likely transmitter of pathogens. They characterized the species as somewhat scarce on carrion and as a secondary invader, appearing after certain sarcophagids, calliphorids, and *M. scalaris*. Brues (1928) found the adults, along with adults of *M. scalaris*, to be frequent visitors to the flowers of *Aristolochia elegans* M. T. Masters in a Cuban garden. Flowers of some members of that genus produce fetid odors.

Of all these reports, only the one by Kloter et al. (1977) gives definitive results of field studies and laboratory rearings of this species. They found that *D. cornuta* larvae tend to embed themselves in the sewage film covering the stones in a trickling filter bed, often becoming completely immersed for long periods while feeding. This burrowing disturbed the anchorage of psychodid larvae, causing their washout by sewage effluent. *D. cornuta* larvae also preyed upon eggs, larvae, and pupae of *Psychoda alternata* Say in laboratory tests, but only when a culture medium for both species, consisting of fresh cow manure with dry yeast, was not provided. In the filter bed, psychodid larvae were easy prey because they clustered permanently in large numbers while only partially buried in the sewage film. While attacking their prey, *D. cornuta* larval mouthparts were protruded and flexed posteroventrally, allowing the phorid to grip its prey against its serrate sternal spatula. Kloter et al. (1977) described the immature stages of *D. cornuta* and illustrated the sternal spatulae and lateral tubercles of first, second, and third instars, the cephalopharyngeal skeleton and four anterior segments of third instars, and the puparium. Some of these illustrations were copied by Ferrar (1987).

Several other authors have also described or illustrated immature stages of *D. cornuta*, and some of the more important contributions are reviewed here. Jones (1918) described and illustrated the egg, third instar and its cephalopharyngeal skeleton, and the puparium, and Cole (1969) reproduced his figures. Patton (1922) illustrated the mature larva and the puparium and its respiratory horns, and Teskey (1981) and Peterson (1987) illustrated the third instar posterior spiracles and the puparium. Schmitz (1941) presented a photograph of the pupal respiratory horns, and he (1938, 1949) described the egg and the third instar and compared them with immatures of other congeneric species. Disney (1983) illustrated the third instar, and Johannsen (1935) illustrated its cephalopharyngeal skeleton. Bohart and Gressitt (1951) presented an illustration of the puparium, and Kaneko and Furukawa (1977) gave detailed illustrations of the third instar and the puparium. De Meijere (1938) illustrated the fine structure of the pupal respiratory horns and described it in detail.

The purpose of this paper is to present observations made while rearing *D. cornuta* through its entire life cycle in the laboratory, and thus to contribute to our understanding of the natural history of a potential disease carrier and our knowledge of the large but little known family Phoridae.

#### MATERIALS AND METHODS

Rearings were kept in ambient laboratory conditions of  $23 \pm 1^\circ\text{C}$  and at least 11 hours of artificial light per day. Paired males and females were held in individual, clear plastic, cylindrical vials ( $5.0 \times 8.5$  cm) fitted with fine wire mesh caps. Mass rearings were held in large ( $19.0 \times 14.0 \times 10.5$  cm) clear plastic boxes in which ventilation holes were cut and outfitted with wire mesh. A layer of moist cotton was placed at the bottom of each rearing container, and food items consisting of fresh and tainted beef liver and a mixture of honey, brewer's yeast, and dehydrated milk mixed in proportions that yielded a thick but tacky aggregate were placed on the cotton. The cotton in the vials was changed every 3–4 days, and the eggs were counted under a dissecting microscope. To obtain eggs of the same age for mass rearings of larvae, glass dishes containing a layer of dry cotton with a piece of tainted liver in the center were placed for a short period in the larger rearing boxes, which contained many gravid females. Four separate mass rearings were observed daily to determine times of molting and puparium formation. Puparia were dropped into individual, glass, 4-dram vials, and they were observed regularly for adult emergence. These vials also contained a layer of moist cotton, and they were plugged with dry cotton.

#### MORPHOLOGICAL CHARACTERIZATION

Eggs, larvae, puparia, and adults are readily recognized. Eggs are elongate-ovoid, shiny white-translucent, and speckled with many minute, white, raised areas. Larvae are yellow to white, with transverse rows of six plumose tubercles situated laterally, dorsolaterally, and dorsally on thoracic segments 2–3 and abdominal segments 1–7, and a pair of minute ventrolateral tubercles on the abdominal segments. Thoracic segment 1 is heavily sclerotized dorsally, and segment 2 has two to six sclerotized patches dorsolaterally in second and third instars. The sternal spatula is serrate anteriorly in all instars. Abdominal segment 12 is margined by six long, plumose tubercles, which are often darkly pigmented, and it bears a pair of dark brown, conical spiracles, which are fused mesially in second and third instars. Puparia resemble third instars in most respects but are yellowish to reddish brown and bear a pair of distinctive, long, pinnate respiratory horns dorsolaterally on abdominal segment 2. Adults of the genus are readily recognized by the forked Rs, single longitudinal setal row on the hind tibia, sensory organ of stout setae on the posterior basal surface of the male's hind femur, and setation on the anepisternum. Of the four known species of *Dohrniphora* in the Nearctic Region, *D. cornuta* is recognizable by the lack of bristles on the hind tibia, the yellow coxae, the lack of a fifth tergite in females, and the distinctive arrangement of about five sensorial setae on the hind femur of males, as illustrated by Borgmeier (1963, Fig. 71) and Peterson (1987, Fig. 62).

#### GENERAL OBSERVATIONS

An opportunity to rear *Dohrniphora cornuta* arose in late September, 1988, when a massive infestation of this fly was discovered in a  $1.8 \times 1.2 \times 1.2$  m wooden box

containing a colony of dermestids used to clean flesh from skeletons. The box was located in the New York State Museum's field research facility in Cambridge, Washington County, New York. Extensive Malaise trapping a few meters from the building throughout the summers of 1985, 1986, and 1988 yielded several thousand specimens of over 50 species of Phoridae, but no *D. cornuta*. Metal racks inside the box held partially cleaned skeletons of many types of vertebrates, and thermostatically controlled light bulbs held the temperature at 21–24°C. The vertebrates had been obtained from various areas of the United States—suggesting the possibility that the phorid was introduced from some other area. The dermestid colony, which was in a state of decline, had been initiated about two years earlier with the larder beetle, *Dermestes lardarius* L. (Coleoptera: Dermestidae), but that species apparently died out and was replaced by *D. vulpinus* Fabricius. The box was also infested with redlegged ham beetles, *Necrobia rufipes* (De Geer) (Coleoptera: Cleridae), and blow flies, *Phaenicia sericata* (Meigen) (Diptera: Calliphoridae).

In nearly two hours of searching for *D. cornuta* larvae and puparia, none were found on the vertebrate skeletons or flesh, although hundreds of adults were flying about. However, a moist, greasy, dark brown mass of decomposing flesh and living and dead insects lined the bottom of the box. This material contained many *D. cornuta* larvae and puparia. Several of the blow fly larvae collected at the same time were dead and covered with living *D. cornuta* larvae, which were consuming them. All other blow fly larvae, including those still alive, showed signs of injury—small brown spots dotting their integument—that might have been caused by the phorid larvae. Phorid puparia were taken to the laboratory, where they were observed for emergence of adults.

#### MATING BEHAVIOR

Adults mated frequently in captivity, often beginning on the day they emerged from puparia. Prior to mating, the male pursued the female, and while they ran about in the distinctive phorid stop-go pattern, the former fanned his wings at frequent intervals. This behavior continued until the male mounted the female. She stood with her wings, which did not reach the tip of her abdomen, in resting position, folded over her abdomen. The bases of the male's hind femora—the areas bearing the so-called sensory organs—came firmly into contact with the pleural plates of the female's seventh abdominal segment, which became laterally compressed. The bases of the male's hind tarsi or apices of his hind tibiae were crossed, and his hind legs were extended posteriorly, usually not touching the female or the substrate. His mid tarsi sometimes clutched the sides of the female's abdomen, and his fore femora were held erect and pressed against his thoracic pleurae and mid femora. The fore tibiae descended at an angle and were loosely crossed, usually suspended above the female's wings. Thus, the relatively small male was mounted at an angle to the female's body, which paralleled the substrate, and he pivoted on the bases of his hind femora with his head rising well above the female. The male stretched his hind legs backward and waved them up and down at a rate of about twice per second, causing his entire body to rock. The apex of the female's abdomen sometimes waved up and down slightly, and the male's hind tibiae were sometimes set into a quivering motion for short periods. The pair remained *in copula* 2–8 minutes, alternating periods of intense rocking with periods of relative calm. The male dismounted when his mate began to run about again, and he was sometimes encouraged with a push from her hind

tarsi. It was not uncommon to find a second female apparently attempting to dislodge a copulating male, usually without success, as Miller (1984) observed in *Puliciphora borinquenensis* Wheeler. Males of both *P. borinquenensis* and *M. halterata* (Wood) attempt to interfere with pairs in stationary matings (Binns, 1980; Miller, 1984).

#### LIFE HISTORY PARAMETERS

Females began to oviposit 1–3 days ( $2.0 \pm 0.5$ ;  $N = 9$ ) after emergence. Eggs were scattered randomly just beneath the surface in relatively dry areas of cotton in the breeding containers. They were not cemented to the fibers and became dislodged easily if the containers were disturbed, thus confirming Jones' (1918) description of the eggs as non-adherent. Kloter et al. (1977) found that *D. cornuta* eggs were deposited in protected crevices free from moisture and sewage film. In the present study, the eggs hatched in about 24 hours. Females laid 77–535 eggs each ( $368 \pm 143$ ;  $N = 9$ ), for an average of 9.4–12.0 eggs per female per day.

Newly hatched larvae quickly found their way to the beef liver, whether it was fresh or tainted. They congregated in areas that were superficially moist and avoided drying areas. They did not burrow into the substrate. Second and third instars frequently burrowed into the surface, leaving only the posterodorsal surface and tubercles of abdominal segment 8, or in some cases only the posterior spiracles, exposed to the atmosphere. In the mass rearing boxes, soft tissues of dead adults were quickly consumed, as was the honey, yeast, and milk mixture. In one trial, a pair of adults was confined with a dead pond snail, *Stagnicola elodes* (Say) (Gastropoda: Lymnaeidae). The female oviposited, and the larvae developed normally and produced viable adults.

The mass rearings of larvae were initiated with over 350 eggs of known age. Little larval mortality occurred. By the second day after oviposition, larvae began molting to the second instar, and by the third day, all larvae were in the second stadium. They began to molt for the second time about the fourth day after oviposition, and all were in the third stadium by the fifth day. On the fifth day they began to leave the food source and wander, and by the eighth day nearly all had formed puparia. Therefore, considering the one-day egg incubation period, it can be inferred that, at  $23 \pm 1^\circ\text{C}$ , the first and second stadia last approximately 1–2 days each, and the third stadium lasts about 3–4 days.

When mature larvae left the food source and began to wander, they became lighter in color. They found a spot in the cotton substrate and came to rest with a thin layer of fibers covering them. After about a day, puparia were formed. Nearly all of them were situated at an angle, with the anterior end higher than the posterior end. Most were on only a slight angle, but in some cases, they were nearly vertical. The fresh, yellowish brown puparia gradually turned to a darker, reddish brown. During the first day, darker, unfocussed, longitudinal lines became visible anterodorsally between thoracic segment 1 and about the level of the dorsocentral tubercles of abdominal segment 2, running along the mesial edge of light colored, raised, circular windows at the anterior end of the latter segment. One to two days after puparium formation, these lines became darker and more sharply focussed. After an hour or two they migrated posteriorly, to about the level of the dorsocentral tubercles of abdominal

segment 4. After 4–5 minutes, the membrane covering the windows swelled slightly and ruptured. The respiratory horns were suddenly thrust out and reached full extension within five seconds after the rupture.

Adults emerged 13–15 days (females:  $14.0 \pm 0.7$ ,  $N = 10$ ; males:  $14.8 \pm 0.4$ ,  $N = 12$ ) after formation of the puparia, or 21–28 days ( $23.4 \pm 4.0$ ,  $N = 260$ ) after oviposition. After emerging, the adults ran about the rearing containers and groomed themselves, but they frequently stopped and rhythmically contracted and expanded their abdomens. Wings were fully inflated about 20–30 minutes after emergence. In newly emerged adults the thorax was yellow except for the proepisternum, postpronotal lobe, upper portion of the anepisternum, and some minute areas at the bases of the wings, which were dark brown. They acquired normal coloration within a few hours.

Jones (1918) found that at  $21.1^{\circ}\text{C}$ , eggs hatched after three days, and the larval and pupal periods were about 16 days each. Bohart and Gressitt (1951) found that at  $29.4^{\circ}\text{C}$  the larval period was over six days, and the pupal period was nine days. The figures reported here for rearings held at  $23^{\circ}\text{C}$  are, as expected, intermediate.

Males lived 4–14 days ( $7.2 \pm 2.2$ ,  $N = 29$ ), and females lived 7–46 days ( $35.0 \pm 12.9$ ,  $N = 9$ ).

#### ADULT FEEDING BEHAVIOR

Adult males, which possess the lapping and sucking type of proboscis, fed most frequently on the honey-yeast-milk mixture, and only rarely were they seen feeding on the liver. Their labella have five pairs of pseudotracheae and lack prestomal teeth (Schmitz, 1938). Females, however, have the piercing and sucking type of proboscis. They fed frequently on the liver and only rarely on the honey-yeast-milk mixture. When the surface of the liver was moist, the females merely applied their labella to it to feed. However, when it was tacky or dried out, they rocked the front ends of their bodies up and down while their probosci were extended. Soon they penetrated the surface and sunk their probosci to a depth of about 0.5 mm, or to about the level of the clypeolabral suture. Females possess four pairs of rudimentary pseudotracheae. The prestomal teeth are large and tricuspid (Schmitz, 1938).

Three females confined in a breeding vial with a live calliphorid larva were found the following day feeding upon the latter, which was now dead. They inserted their probosci into the larva's oral pocket or folds in its integument. They were successful in piercing the integument of the larva's cephalic segment. It is not entirely clear whether or not the flies caused the larva's death, and unfortunately it was not possible to repeat the trial. Females were also successful in piercing the integument of dead adults of their own species, which they consumed. On several occasions, females were found feeding on larvae of their own species, and on at least one occasion a female was found with a living first instar suspended from the tip of her proboscis, suggesting that she was trying to feed on the larva. Schmitz (1938, 1951) mentioned a case in which an English physician in Brazil claimed a female of *D. cornuta* attempted to bite him, and he felt a prick. However, in seven man-hours that three people worked with the abovementioned, heavily infested box, no bites were reported, and swarming around the face was not noticed.

## DISCUSSION

The catholic feeding habits and synanthropic tendencies of *Dohrniphora cornuta*, like those of *Megaselia scalaris*, *Spiniphora bergenstammi* (Mik), and probably some other phorid species, have undoubtedly contributed to its wide distribution and pest status. These three species are mentioned here because it has been found an easy matter to rear large populations of all of them in the laboratory on beef liver (unpubl.). Apparently, however, *D. cornuta* is never the nuisance that *M. scalaris* is capable of being. The latter species has been reported several times as causing cutaneous, ophthalmic, intestinal, and urogenital myiasis in man, and it is frequently found in animal carcasses and human and animal excrement (James, 1947; Biery et al., 1979; Singh and Rana, 1989). On 9 December, 1988, Dr. Stuart L. Dawson of the Office of the Medical Examiner, Suffolk County, New York, found *M. scalaris* breeding on a black and tarry, partially skeletonized corpse that had been buried in Aguas Buenas, Puerto Rico, for about one year (S. L. Dawson, pers. comm.). *D. cornuta* has somewhat less revolting habits; apparently, it has never been reported as the cause of human myiasis, and it has not been found in human corpses. *S. bergenstammi* is even less of a pest, although it is frequently reported by public health authorities in Great Britain from improperly washed milk bottles (Disney, 1983).

Studies of mating behavior in the Phoridae are exceedingly rare. In *M. scalaris*, copulation is usually preceded by a prolonged period of courtship during which the male makes complex wing and leg movements. Tandem flights of mating pairs have been observed. Such phoretic copulation is common in *Puliciphora borinquenensis*, a species that breeds in small patches of decomposing organic matter, such as dead insects. In this species, the females are small and apterous and there is little observable courtship. A male simply pounces upon a female, grasps her abdomen with his middle tarsi while his hind tarsi remain on the substrate, and attempts to mate. During copulation, the male rapidly vibrates his forelegs on either side of the female's head and thorax. The male frequently airlifts the female and seeks a new oviposition site (Miller, 1978). Miller (1984) described additional reproductive routines in which the male performs a rapid sequence of stationary copulations with "parading" (or "calling," suggesting the diffusion of a pheromone) females at the emergence site, the male mates on a new oviposition site with a recently arrived female, and the male airlifts a female from the emergence site and randomly deposits her when a new site cannot be found. Males can learn the locations of new oviposition sites, transport large numbers of females, guard recently deposited females against mating with other males, and switch routines. Observations on *Megaselia halterata*, a pest in mushroom houses, suggest that mating always takes place on a surface, males display around a single, stationary, calling female by running in arcs and circles while alternately vibrating and trailing their wings, that male display soon terminates when a single male wins in competition with several others for the right to copulate, and that pairs frequently fly *in copula* (Binns, 1980).

In the present observations of *Dohrniphora cornuta*, mating appears to be a much simpler process, with a brief display and chase by a male, followed by coupling. The fact that all observations were made in severely confined, and sometimes crowded, rearing containers suggests the possibility that a full range of routines was not displayed. Flight was minimal in the confined quarters, and food was always abundant.

It is therefore reasonable that prolonged courtships and copulatory flights would not be observed. Perhaps under sparser and more stressful conditions a fuller range of behaviors would be observed. On the other hand, *D. cornuta* might not have a fuller repertoire. Perhaps it specializes in using more stable resources than *P. borinquenensis* and *M. halterata* do, rendering competition for mates and specialized mating behaviors less necessary.

There are over 100 known species of *Dohrniphora*, most of them from the Neotropical Region, and they are most readily distinguished by the arrangement of spines or setae and the diverse lobes and ridges at the base of the posterior face of the male hind femur (Borgmeier, 1968; Borgmeier and Prado, 1975). Borgmeier (1960, 1961, 1963) referred to these areas as "Sinnesorganen" or "sensorial organs." The heretofore unreported observations that these areas contact the pleurites of the female's seventh abdominal segment and act as a pivot while male *D. cornuta* perform an elaborate copulatory rocking behavior suggest that they have a stimulatory, or courtship, function, rather than a sensorial function. According to Eberhard's (1985) hypothesis of sexual selection by female choice, a similar function is assumed for the elaborately evolved male genitalia found in many, perhaps most, groups of animals. The function of these structures, in other words, is not just insemination, but to induce the females to receive and use the sperm. Perhaps a better term for the complex, femoral areas is "stimulatory patches."

The tremendous diversity of form suggests rapid and divergent evolution of stimulatory patches and male genitalia relative to other structures. According to the hypothesis, males with mechanically superior sexual structures or better stimulating devices are favored, and females that preferentially allow such males to fertilize their eggs are also favored. The consequence is that runaway sexual selection by female choice on male sexual structures results in both rapid and divergent evolution. On the other hand, females evolve new and more effective neural properties and remain relatively uniform structurally. At the present time we lack evidence relating to rapid and divergent evolution of male genitalia in *Dohrniphora*, although it seems likely based upon our knowledge of other phorine genera. We also lack documented evidence that female sexual structures are relatively uniform, although nothing in the literature suggests otherwise. Further examination of these structures and studies of the mating behavior of other species in the genus could help shed some light on Eberhard's hypothesis.

Among the unfortunately few in-depth phorid life history studies that exist, some fairly common patterns emerge. As in *Dohrniphora cornuta*, females of many species, including *Puliciphora borinquenensis*, have better developed mouthparts than males. Males of both species live only about one fifth or one quarter as long as females. Males of the latter species were never observed feeding, even after eight years of being cultured at the University of Oxford (Miller, 1984). Life history parameters are similar among several species that have been studied, including *Megaselia aequalis* (Wood) (Robinson and Foote, 1968), *M. scalaris* (Loew) (Robinson, 1975), and *Gymnophora luteiventris* Schmitz (Brown, 1985). As in *D. cornuta*, eggs of these three species hatch about 24 hours after oviposition, larvae require about 9–10 days to mature at room temperature, and adults emerge 10–15 days after puparium formation. Also as in *D. cornuta*, the pupal respiratory horns of *M. aequalis* appear about 24 hours after pupariation (Robinson and Foote, 1968).



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